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INTRA- AND EXTRA-PAIR COPULATIONS AND FEMALE REFUSAL OF MATING IN MONTAGU'S HARRIERS

MASSIMO PANDOLFI, ROBERTO PAGLIARANI AND GIANCARLO OLIVETTI

University of Urbino, Istituto di Scienze Morfologiche, Via M. Oddi, 21-61029 Urbino, Italy

ABSTRACT.—We studied the mating behavior of Montagu's Harriers (*Circus pygargus*) and recorded the incidence of extra-pair copulations (EPC) and refusal of females to copulate. The average duration of copulations was 4.9 sec and they were most frequent between 1000–1400 H. Each pair averaged 105 successful copulations per clutch (range = 31–245). About 59% of 114 within-pair copulation (WPC) attempts were unsuccessful and, in 14 cases, the female rejected its mate. For the majority of cases, the cause of copulation failure was not identified. While the frequency of copulation attempts was not correlated with food-pass frequency, the duration of copulations was influenced by the presence of food brought by the male. Copulation attempts peaked early in the breeding season (3 wk prior to the beginning of egg laying) and outside the fertile period of females. Successful copulations peaked early in the breeding season (wk 4) and during the females' fertile period (wk 1). Copulation early in the breeding season may function to assess male competence in Montagu's Harriers allowing a way for females to evaluate the quality of males. Refusal is an aspect of female behavior that could help us to understand if, and in what way, female choice is based on the capacity of the male to successfully transfer sperm.

KEY WORDS: *Circus pygargus*; *Montagu's Harrier*; *copulation*; *extra-pair copulation*; *copulation refusal*.

Intra- and extra-pair copulations y rechazo de la hembra de ser montada en el Aguilucho Cenizo

RESUMEN.—El motivo de este estudio es de presentar observaciones de las montas del Montagu's Harriers (*Circus pygargus*) y de discutirlo en relación a extra-pair copulations (EPC) y el rechazo de la hembra de ser montada. La media de duración de la monta era 4.9 y las cópulas eran más frecuentes entre 1000–1400 H. Cada pareja lleva a cabo una media de 105 cópulas exitosas por puesta (rango = 31–245). Alrededor del 59% de 114 WPC intentos fueron fallidos y en 14 casos observamos que la hembra rechazaba su macho. Para la mayoría de los otros casos no identificábamos cual era la causa del fallo en la cópula. La frecuencia de los intentos en la copulación no está correlacionada con la frecuencia de transferencia de alimentos, pero la duración de las copulaciones se ha encontrado que está influenciada por la presencia del alimento llevada por el macho que lleva a cabo la mayoría de los intentos cuando la probabilidad de éxito es mayor, y por tanto cuando la hembra ha recibido o está comiendo la presa. La variación estacional en los intentos de cópula muestran un pico temprano en la temporada de cría (tres semanas antes de la deposición de los huevos, o semana 3) y fuera del periodo fértil de la hembra. La frecuencia exitosa de cópulas muestran dos picos: uno temprano en el periodo reproductor (semana 4) y otro durante el periodo fértil de la hembra (semana 1). Por lo tanto, la cópula, especialmente aquellas durante las etapas tempranas del periodo reproductor, pueden tener una función social importante en el Montagu's Harrier. Para la hembra pudiera ser una forma de evaluar la calidad del macho y el rechazo es un aspecto del comportamiento de la hembra, que podría ayudarnos a entender si, y en que manera, la elección de la hembra está basada en la capacidad del macho para alcanzar cópulas exitosas.

[Traducción de Fernando Hiraldo]

The Montagu's Harrier (*Circus pygargus*) is generally monogamous (Cramp and Simmons 1980) but occasionally is polyandrous (Pandolfi et al. 1995, Arroyo 1996) or polygynous (Hens 1926 in Cramp and Simmons 1980, Dent 1939, Underhill-Day 1990). Its copulation behavior is relatively unknown. In monogamous species investing heavily in parental care, Trivers (1972) predicted that natural selection should favor males that pursue a mixed reproductive strategy. Therefore, males increase their fitness by mating with and fertilizing females that have already mated and whose young will be reared without their help. The benefits of extra-pair copulations (EPC) for females are not as clear, especially when females actively resist (McKinney et al. 1984). On the other hand, females apparently go in search of EPCs and data suggest that they sometimes solicit EPCs from males with higher quality than their partners (Birkhead and Møller 1992, Kempenaers et al. 1997). Numerous instances have been reported of females refusing to mate with their partners (Indigo Buntings [*Passerina cyanea*], Westneat 1987; Tree Swallows [*Tachycineta bicolor*], Venier and Robertson 1991; White Storks [*Ciconia ciconia*], Tortosa and Redondo 1992; Willow Warblers [*Phylloscopus trochilus*], Arvidsson 1992; Red-billed Gulls [*Larus novaehollandiae*], Mills 1994; Razorbills [*Alca torda*], Wagner 1996; Ospreys [*Pandion haliaetus*], Birkhead and Lessells 1988; African Marsh-Harriers [*Circus ranivorus*], Simmons 1990; Black Kites [*Milvus migrans*], Koga and Shiraishi 1994).

This study was undertaken to observe the mating behavior of Montagu's Harriers in reference to EPCs and refusals by females to copulate.

STUDY AREA AND METHODS

We observed the behavior of the Montagu's Harrier at two sites in the Pesaro-Urbino area (Monte della Mattered: 43°46'20", 12°51'20" and Montefabbri: 43°46'00", 12°40'50"), Marche region, Italy from 1991-96. Breeding sites were in the foothills of the Apennines (altitude 200-500 m) and consisted of uncultivated steep badlands and wheat crops.

Four to six pairs of Montagu's Harriers nested in loose colonies at the two sites. Individuals were identified by molt and plumage color and consistent use of perches. We were able to identify individual birds in six of the 24 pairs studied and only data derived from these six pairs are presented. We collected 512 hr of observations on these six pairs from the time they arrived at nesting sites until the time they left. Observations were made between sunrise and sunset for five consecutive hours of observation each day. This allowed us to cover all daylight hours over the period of one week with three shifts. Ob-

servations were made using 10×50 binoculars and a 30× spotting scope.

The term copulation attempt was used to refer to copulation attempts by males regardless of their success. We assumed that the time needed for the male to balance on the back of the female before cloacal contact was at least 3 sec; therefore all attempts lasting <4 sec were classified as unsuccessful (Simmons 1990). Copulation attempts were considered as individual cases even if they occurred during a succession of attempts by the male. Refusals to mate by females were only counted if we were certain that their behavior did not allow males to land on their backs, or if their behavior caused males to lose their balance and take flight within 1 sec.

In birds, the length of the female's fertile period depends on various factors: duration of sperm storage in the female reproductive tract, time interval between the fertilization of an egg and its subsequent deposition, and number of days in which the clutch is completed (Birkhead 1988, Birkhead and Møller 1992). The duration of sperm storage and the time interval between fertilization of an egg and its subsequent deposition have not yet been established in the Montagu's Harrier; therefore, in order to hypothesize the duration of the presumed female fertile period, we used data for the American Kestrel (*Falco sparverius*, Bird and Buckland 1976), where the duration of sperm storage in the female lasts about 8 d. We assumed that sperm storage in female Montagu's Harriers was about 6 d prior to egg laying, given that this is the shortest period of sperm storage known (Birkhead and Møller 1992). The time between ovulation and deposition of an egg is about 24 hr in domesticated fowl (Birkhead and Møller 1992). Fertilization takes place within one hour of ovulation, so we assume a period of one day between fertilization and egg deposition for the Montagu's Harrier. We assumed that the female fertile period began on the seventh day (6 + 1) before the deposition of the first egg and ended about one day before the deposition of the last egg. Egg laying was determined by observing nests with the aid of a mirror which allowed us to see the eggs while maintaining a distance of about 3 m from the nest. We counted back 29 d (Cramp and Simmons 1980) from the date of hatching in order to obtain the date on which egg laying occurred. The date of hatching was estimated by counting back from the age of the oldest chick which was estimated from morphological characters (Cramp and Simmons 1980). We assumed an average of 2 d between laying of each egg (Cramp and Simmons 1980, Glutz et al. 1971).

We divided the reproductive season into weeks, calling the week in which eggs were laid wk 0. The courtship period included wk -4, -3, -2; the presumed female fertile period was wk -1 and wk 0. We assumed that egg laying started on first day of wk 0.

We recorded behavior 5 min before and 5 min after copulation attempts. Because both males and females can show more than one display during this 5-min period, the proportion of each display type (expressed as a percentage) exceeded 100%. The various displays are defined in Pandolfi and Pino D'Astore (1990). With the term "sky-dance" we mean sky-dancing plus spiraling *sensu* Simmons (1991).

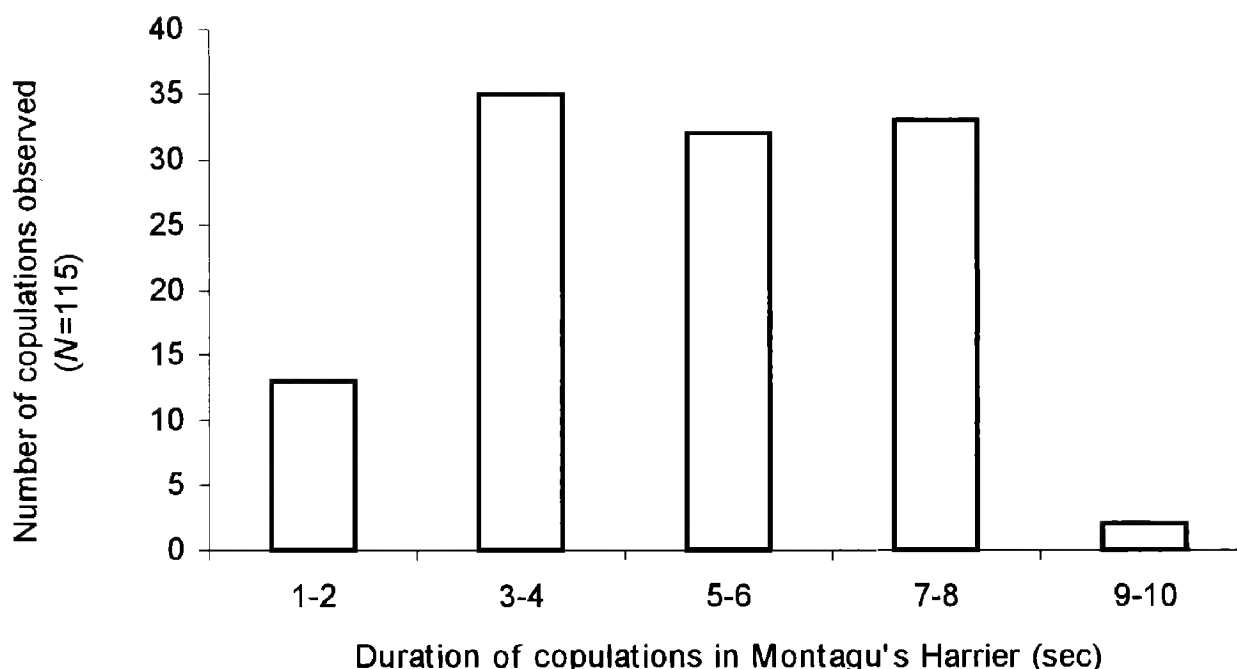


Figure 1. Duration of copulations in Montagu's Harriers in the Pesaro-Urbino area, Italy.

RESULTS AND DISCUSSION

Montagu's Harriers mated on the ground (89% of 111 copulations) and on perches such as poles or shrubs (11%). Prior to copulation, the most frequent activity observed involving both members of the pair was a food pass (48% of 94 cases). In 17% of the cases, the pair had previously performed copulation, while in 5% of the cases there had only been flight play. Males were perched in breeding areas in 14% of the cases and in 28% of the cases for females. Males performed a sky-dance in 1% of

cases, and showed intraspecific aggressiveness in 5% of the cases. In four of these cases, males attacked other males (three neighbors and one not identified) and, on one occasion, a male attacked a female neighbor.

Males flew in front of females and turned sharply (in a hook-flight) to land on their backs. If males came from behind, they simply glided onto the females' backs. Males balanced themselves by stretching out and beating their wings while females lowered and raised their tails to allow cloacal contact.

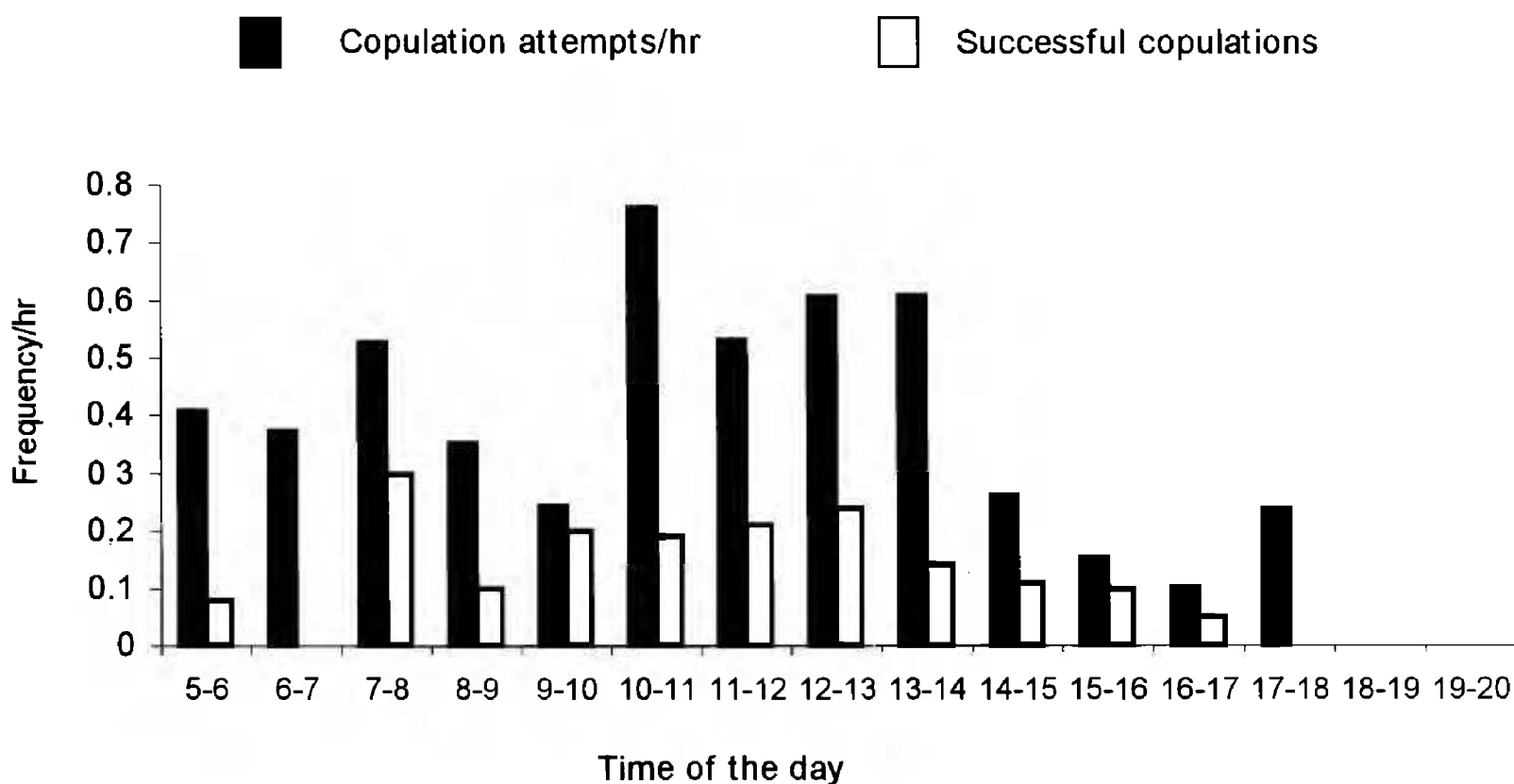


Figure 2. Diurnal fluctuation in frequency of copulation in Montagu's Harriers in the Pesaro-Urbino area, Italy

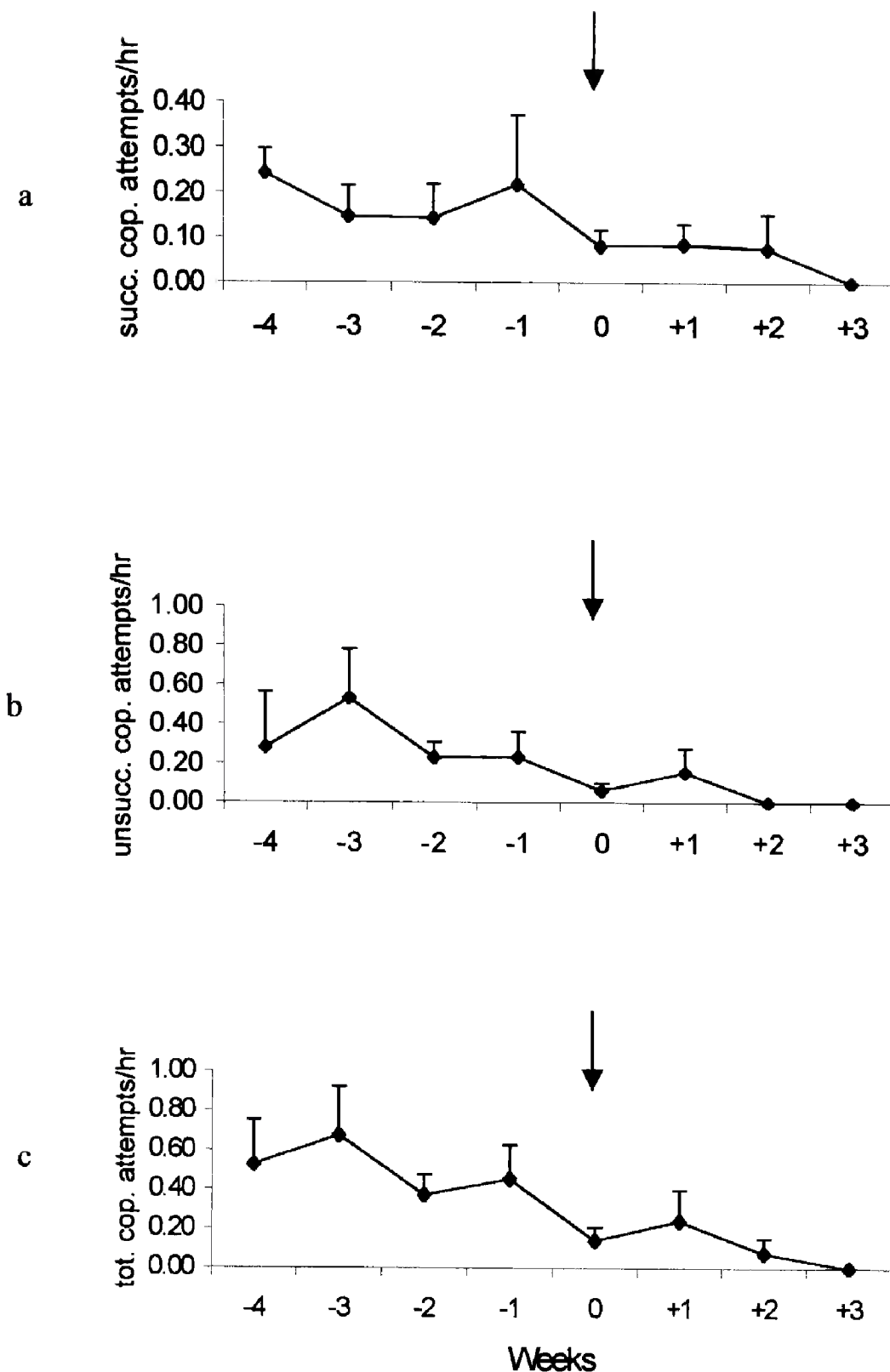


Figure 3. Seasonal variation in successful (a), unsuccessful (b) and total copulation attempts (c), relative to the beginning of egg laying (\downarrow) in Montagu's Harriers in the Pesaro-Urbino area, Italy. Y-axes show means and SE.

The average duration of successful mounts was 4.9 sec (SD = 2.1; $N = 115$) and 87% of 115 copulations lasted between 3–8 sec (Fig. 1). There were no significant differences (Kruskal-Wallis test, $H = 0.1085$, $df = 2$, $P = 0.09$) in the duration of copulations between the three time periods into which we divided the day (dawn–0900 H, 0900–1400 H, and 1400 H–sunset).

Following each copulation, both males and females perched in the area in the majority of 94 cases (53% for males, 69% for females). In 15% of

the cases, there was further copulation. In 21% of these, males left nesting areas while females left in 9%. In the remaining cases, we recorded activities such as intraspecific aggressiveness (3% for males: two cases toward other males and one case toward a female; 2% for females: one case toward another female), flight play (1%), and other behaviors (9% for males, 4% for females).

Copulation attempts occurred unevenly throughout the day ($\chi^2 = 16.10$, $df = 6$; $P < 0.05$), showing a higher frequency between 1000–1400 H.

After 1400 H, there was a marked reduction in copulation frequency, apart from a smaller peak between 1700–1800 H (Fig. 2).

The seasonal trend in copulation attempts carried out by males showed a peak during the courtship period in wk -3 (3 wk prior to the beginning of egg laying) when 0.68 copulation attempts/hr was recorded. Another smaller peak occurred in wk -1, with 0.45 copulation attempts/hr (Fig. 3c). We found a significant difference in the total copulation attempts/hr during the various weeks (Kruskal-Wallis test $H = 17.44$, $df = 7$, $P = 0.0147$) with a constantly decreasing trend from wk 4 to wk +2, after which no further copulation attempts were recorded in the six focal pairs.

The frequency of successful copulations peaked at 0.24 copulations/hr during wk -4, with a second peak of 0.22 copulations/hr during wk -1 (Fig. 3a) but copulation frequency did not vary significantly over time (Kruskal-Wallis test $H = 9.37$, $df = 7$, $P = 0.2271$). Both Goshawks (*Accipiter gentilis*) (Møller 1987) and Lesser Kestrels (*Falco naumanni*) (Negro et al. 1992) show a similar bimodal pre-egg laying peak in copulations.

The frequency of unsuccessful attempts was very high during the courtship period and decreased after wk -1 (Fig. 3b). The variation in frequency between the various weeks was statistically significant (Kruskal-Wallis test $H = 16.13$, $df = 7$, $P = 0.0239$).

During the courtship period (21 d, wk -4, -3, -2) and the presumed female fertile period (13 d for a modal clutch of four), we observed 40 successful copulations during 192 hr of observations, yielding a frequency of 0.2 successful copulations/hr. Considering that daily harrier activity spans 15 hr, each pair ($N = 6$) successfully copulated about 102 times per clutch (range = 31–245). The range was very wide but was comparable with other raptors. In fact, for the African Marsh-Harrier (*Circus ranivorus*), Simmons (1990) estimated 37–160 successful copulations per clutch whereas Birkhead and Lessels (1988) reported a range of 20–97 successful copulations per clutch for Osprey.

Copulations during the courtship period occurred outside the female fertile period. In other species of raptors, copulations have been recorded both during and outside the female fertile period: Goshawks (Møller 1987), Cape Vultures (*Gyps coprotheres*) (Robertson 1986), Ospreys (Birkhead and Lessels 1988), African Marsh-Harriers (Simmons 1990), Merlins (*Falco columbarius*, Shodi 1991),

Lesser Kestrels (Negro et al. 1992) and Black Kites (*Milvus migrans*, Koga and Shiraishi 1994).

Various explanations have been given to explain copulation in the early stages of the breeding season. For example, males may try to copulate early on in the pre-laying period to increase their paternity insurance, given that it is not certain when the female will lay the first egg (Birkhead and Møller 1992). Alternatively, it may be in the female's interest to hide her fertile period to exchange copulations for food (Møller 1987). The latter hypothesis is not very probable for Montagu's Harriers, as there is no relation between the hourly rate of successful copulations and the hourly rate of food passes during these weeks (Spearman correlation coefficients $r_s = 0.1567$, $N = 30$, $P = 0.408$). Another possibility is that copulation attempts at the beginning of the breeding season are part of an evaluation mechanism by females (Tortosa and Redondo 1992). They could also function to establish and maintain the pair bond (Newton 1979), given that Montagu's Harriers remate every year (Cramp and Simmons 1980).

The peak of successful copulations during wk -1 corresponded to the presumed female fertile period and might be explained both by fertilization and sperm competition hypotheses. In fact, most harriers produce unhatched eggs (Simmons 1990) and the six pairs that we studied produced 25 eggs, 20% of which did not hatch. This suggests that frequent copulation limits infertility of eggs while diluting the sperm of other males. Hatching failure might also be due to defects in eggs rather than a lack of sperm, but we do not have information on this possibility.

Given that copulations recorded during the incubation period continued until wk +2, they may function to provide sperm for replacement clutches in the case of nesting failure, as suggested by Birkhead et al. (1987). They may also serve to maintain the pair bond. Because only males engage in play and feeding activity with young during the post-fledging period (Giacchini and Pandolfi 1994, Pandolfi 1996), the pair bond is probably weakened. This could explain why copulations were not recorded later in the breeding season as happens in Cape Vultures (Robertson 1986), Goshawks (Møller 1987) and African Marsh-Harriers (Simmons 1990). For Cape Vultures, pair bonds are lifelong (Robertson 1986) and African Marsh-Harrier pairs bond for >1 yr (Simmons 1990). The Goshawk is a nonmigratory species and pair bonds

certainly last longer than in the migratory Montagu's Harrier.

Of 118 copulations we observed, 4 EPC attempts were observed (3.4%). EPCs involved two extra-pair males, and two females that belonged to focal pairs. Two EPCs occurred 7 d before the start of egg laying, while the other two occurred 2 d before egg laying. All four attempts occurred during females' presumed fertile periods (two females involved). Two of the four EPCs were successful (i.e., the male stayed on the back of the female for ≥ 4 sec). In three of the cases, the female's mate was absent. In the one case when her mate was present, his behavior showed indifference, but the EPC was unsuccessful. Females never rejected the attempts of the extra-pair males and all females were already mated in the colony. One of the males involved already had a mate and belonged to the colony, while the other was not identified. The percentage of EPCs recorded in our study was slightly less than that reported by Arroyo (1996) for Montagu's Harrier in Spain. The fact that the four cases we observed all fell within the presumed female fertile period and that females never resisted suggests that this strategy effectively allows pursuing males, even only occasionally, to increase their reproductive success at the expense of others. Although Simmons (1990) reported an EPC of 2% in African Marsh-Harriers, he found that the males copulated more frequently when they nested in colonies. His finding supports the sperm competition hypothesis suggesting that such a low number of EPCs could trigger mechanisms of sperm competition benefiting those males that use them and take the necessary countermeasures. Montagu's Harrier males spent more time ($\chi^2 = 59.94$, $df = 1$, $P < 0.01$, Yates corrected) in the nesting area near their partner during the female fertile period (43%) than during wk +1, +2, +3 (35%), a pattern that is common in other raptors such as African Marsh-Harriers (Simmons 1990), Ospreys (Birkhead and Lessells 1988) and Goshawks (Møller 1987). Behaving in this way, males may deter access to females by other males (Birkhead and Lessells 1988). This form of male mate-guarding could explain the low proportion of EPCs observed.

For females, the risks regarding the loss of parental care (Trivers 1972) could be minimized if the intruder were to carry out the EPC attempts in the absence of their males, as in fact happened in three out of four cases we observed. The fact that the females did not dissuade these males suggests

that they already knew these males and they were of "high quality." Even though one of the two males was unidentified, it probably belonged to the colony under observation, which comprised five pairs during the reproductive season. The risks could be too high for females accepting EPCs from unknown males since a male of unknown quality could fertilize their eggs (Birkhead and Møller 1992). However, females may gain by increasing the genetic quality or diversity of chicks (Birkhead and Møller 1992). Indeed, numerous cases have been recorded of broods not genetically related to their putative father (Avisé 1996). Data available on raptors suggests that this phenomenon is not widespread (Swatschek et al. 1994, Korpimäki et al. 1996, Negro et al. 1996) but is present nonetheless.

In 48% of 94 cases, food passes occurred 5 min before copulations. However, copulation frequency was not correlated with food passes during the first six weeks of the breeding season (Spearman correlation coefficient, $r_s = 0.16$, $N = 30$, $P = 0.4$). There was also no significant correlation between the frequency of successful copulations and food-pass frequency over the various weeks ($r_s = 0.1567$, $N = 30$, $P = 0.408$). These data are similar to those found by Picozzi (1984) for Hen Harriers (*Circus cyaneus*) and by Simmons (1990) for African Marsh-Harriers that showed food passes to be important, but not essential, correlates of copulation. Consequently, we examined whether the duration of a copulation was influenced by the presence of food provided by males. The median duration of copulation attempts when food was present (4 sec) was significantly higher than the median duration of copulation when food was not present (0 sec, Mann-Whitney U -test, $U = 691.5$; $P = 0.01$). This difference remained significant even when only attempts in which males effectively landed on females' backs (food present median = 5 sec; food absent median = 3 sec; $U = 152.5$; $P = 0.0496$).

When food was present, males were successful in 29 out of 56 cases (52%); without food, only 5 out of 35 attempts (14%) were successful ($\chi^2 = 11.39$, $df = 1$, $P < 0.01$, Yates corrected). Of 91 attempts, 56 (62%) were carried out in the presence of food, while 35 (38%) were attempted in the absence of food, a difference that is statistically significant ($\chi^2 = 4.4$, $df = 1$, $P < 0.05$, Yates corrected). Therefore, the duration of copulations was influenced by the presence of food brought by males and they attempted copulations when the probability of success was highest (i.e., when females had received

or were eating prey). For African Marsh-Harriers, Simmons (1990) found that, while food was not a prerequisite for copulation and did not even influence the duration, males had a higher probability of being unsuccessful if food was absent. For Ospreys, Poole (1985) reported that feedings were not an immediate stimulus for copulations but that efficient food transfers among courting Ospreys appeared to be a requirement for successful copulations.

We observed 14 copulation rejections by female harriers in 114 within-pair copulations, 47 (41%) of which were successful. This was considerably lower than the 73% estimated for African Marsh-Harriers (Simmons 1990). The unsuccessful attempts resulted directly from the female's behavior. In the other 53 cases, two of the failures were attributable to external factors (e.g., males left to fight off female intruders or left to fight off crows [*Corvus* spp.]). For the remainder of cases we could not identify the reason for the copulation failure.

Of the 14 cases in which the female refused to copulate, 13 occurred during courtship and only one occurred during fertile period. The possibility that females simply were not physiologically ready is little supported by our data. In fact, from the beginning of the courtship period, we observed successful copulations (Fig. 3). During the daytime, 10 out of 14 refusals were observed between 1000–1400 H, when the frequency of successful copulation attempts/hr was high (Fig. 2). In four cases food was present, in six it was absent, and in the remaining four cases the presence or absence of food was unrecorded. We have no data on prey size in these cases, so we cannot control for any correlation between prey size and female refusal.

We observed the following female behaviors during copulation refusals: in four cases, males had begun landing when females lay flat on the ground keeping their wings semiopen and flattened with their tails toward the ground; in seven cases, females opened and beat their wings; a female flew away once; once a female jumped away; and once a female hit the male with her talons claws while landing. The first behavior was also described by Studinka (1942) as soliciting behavior for copulation by the female. We interpreted this as a refusal because when examining the 13 cases in which females behaved in this way (seven cases observed in two out of the six focal pairs and six cases observed in two other pairs), the male copulated successfully

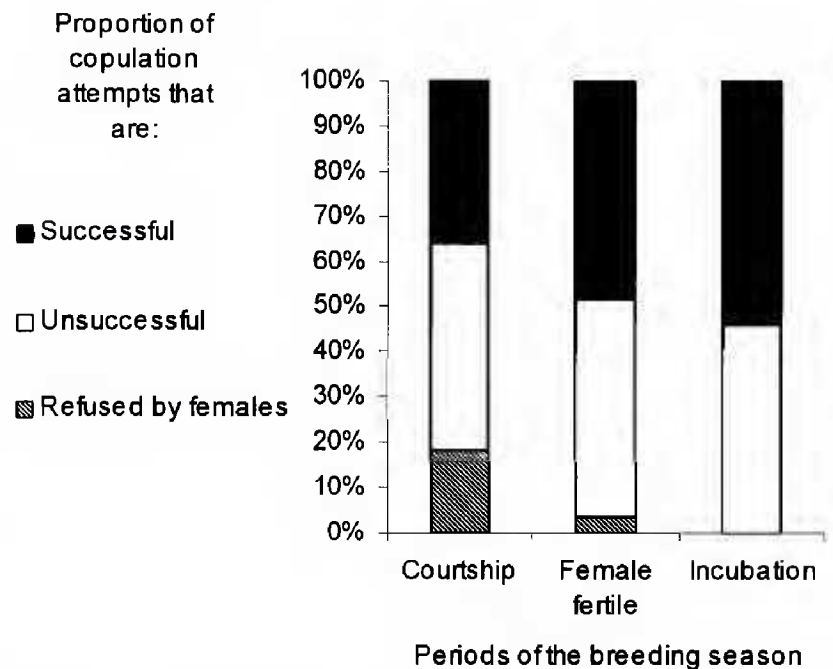


Figure 4. Proportion of successful and unsuccessful copulation attempts and refusal by female Montagu's Harriers during various periods of the breeding season in the Pesaro-Urbino area, Italy.

on only one occasion. Sudden opening of wings by the female followed by flattening on the ground are movements which make it difficult for males to land. The fact that females spread their tails toward the ground could have been a signal indicating unwillingness to copulate since the tail must be raised for cloacal contact.

Even though there was not a significant difference between the proportion of successful copulation attempts, copulation attempts that failed because of refusal by the female, and those that failed for other reasons during the three periods considered ($\chi^2 = 6.71$, $df = 4$, $P > 0.05$) females refused 18% of the attempts by the males during the courtship period and refused only 3% of attempts during their presumed fertile period (Fig. 4). The increase in the proportion of successful copulations during the fertile period appeared to be due, at least in part, to the lower number of female refusals. Simmons (1990) reported nine (4.6%) cases of refusal by female African Harriers out of 196 attempted copulations. This rate is similar to that reported by Koga and Shiraishi (1994) for Black Kites, where 4.1% of 246 copulation attempts were refused by females. In both cases, however, the periods in which refusals took place were not reported.

In White Storks (*Ciconia ciconia*, Tortosa and Redondo 1992) and Lesser Kestrels (Negro et al. 1996), males copulate frequently even in the absence of sperm competition. It has been suggested

that these males may advertise their good condition by performing energetically costly copulations; therefore, copulations are part of a process of mate assessment involved in the acquisition and maintenance of the pair bond (Tortosa and Redondo 1992, Negro et al. 1996). This may also be the case in the Montagu's Harrier. Intense copulation activity carried out by males despite female refusals could serve to indicate the general health of males, assuming that copulations are expensive in terms of sperm production and physical courtship activity (Dewsbury 1982). Furthermore, in refusing, females could test the ability of males to copulation and fertilization. A rather long period would be advantageous to establish the quality of males in order to limit the risks of being deceived. If these characteristics were inherited, it would be advantageous for females to fertilize her eggs with these males (Birkhead and Møller 1992).

In conclusion, while the frequent copulation pattern observed in Montagu's Harrier may be explained with the sperm competition hypothesis, copulations may also have an important social function during the courtship period. For females, it could be a way of evaluating the quality of males. Therefore, refusal is an aspect of female behavior that could help us to understand if, and in what way, female choice is based on the capacity of males to transfer sperm.

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